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Theta Activity from Frontopolar Cortex, mid-Cingulate Cortex and Anterior Cingulate Cortex Shows Different Role in Cognitive Planning Performance

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ABSTRACT

Cognitive planning, the ability to develop a sequenced plan to achieve a goal, plays a crucial role in human goal-directed behavior. However, the specific role of frontal structures in planning is unclear. We used a novel and ecological task, that allowed us to separate the planning period from the execution period. The spatio-temporal dynamics of EEG recordings showed that planning induced a progressive and sustained increase of frontal-midline theta activity (FMθ) over time. Source analyses indicated that this activity was generated within the prefrontal cortex. Theta activity from the right mid-Cingulate Cortex (MCC) and the left Anterior Cingulate Cortex (ACC) were correlated with an increase in the time needed for elaborating plans. On the other hand, left Frontopolar cortex (FP) theta activity exhibited a negative correlation with the time required for executing a plan. Since reaction times of planning execution correlated with correct responses, left FP theta activity might be associated with efficiency and accuracy in making a plan. Associations between theta activity from the right MCC and the left ACC with reaction times of the planning period may reflect high cognitive demand of the task, due to the engagement of attentional control and conflict monitoring implementation. In turn, the specific association between left FP theta activity and planning performance may reflect the participation of this brain region in successfully self-generated plans.

Keywords: planning; frontal midline theta frequency band (FMθ); prefrontal cortex; frontopolar cortex, mid-cingulate cortex; anterior cingulate cortex; cognitive control.

1. INTRODUCTION

Cognitive control or executive functions are a theoretical construct that includes a wide range of higher-order cognitive functions associated with goal-directed behavior (Lezak, 1995; Shallice, 1991; Stuss, 1992; Zwosta, Ruge & Wolfensteller, 2015; Cooper, 2010). One of these functions is planning (Collins & Koechlin, 2012; Sira & Mateer, 2014; Lunt et al. 2012), which consists of the ability to develop a sequenced plan to achieve a goal in an organized, strategic and efficient manner (Hayes-Roth & Hayes-Roth, 1979). Planning allows imagining what the future might be and how our behavior could affect and change the current state leading us to this imagined future (Benson, 1993). The extent of plans can range from simple motor behaviors (e.g., planning a sequence of key presses) (Pascual-Leone et al., 1993) to a highly demanding cognitive task (e.g., deciding on the steps required to land an airplane) (Suchman, 1987). Planning behavior can be divided into two major phases: *i)* a mental planning phase that involves elaborating an internal representation of a sequence of steps (plans) (Wilensky, 1983) and *ii)* a planning execution phase that involves the motor action to achieve a previously planned goal (Grafman & Hendler, 1991). Thus, planning can be measured in simple and/or more complex tasks (Schwartz et al., 1991). Typically, in the context of higher-order cognitive processes, planning requires the operation of several components of the executive functions (e.g., working memory, attentional control, response inhibition) making the experimental manipulation and its isolated measurement difficult (Hayes-Roth & Hayes-Roth, 1979; Tremblay et al., 1994).

Neuroimaging studies have provided valuable evidence about the critical role of the Prefrontal Cortex (PFC) in cognitive control, including planning. Several studies have suggested a relevant implication of the dorsolateral PFC (Nitschke et al., 2017; Morris et al., 1993; Owen et al., 1996; Baker et al., 1996; Dagher et al., 1999; Newman, 2003; Kirsch et al., 2006), the Frontopolar cortex (FP) (Braver & Bongiolatti, 2002; Baker et al., 1996; Christoff & Gabrieli, 2000), the mid-Cingulate Cortex (MCC), and the superior parietal lobe, among other brain regions (Kirsch et al., 2006; Newman, Carpenter, Varma, & Just, 2003; Owen, Doyon, Petrides & Evans, 1996) using behavioral paradigms such as Tower of London (Shallice, 1982; Unterrainer et al., 2004) or Porteus Maze (Porteus, 1959; Gallhofer, Bauer, Lis, Krieger, & Gruppe, 1996; Krieger, Lis, & Gallhofer, 2001; Lee et al., 2007; Lezak, 1995; Peters & Jones, 1951; Tremblay et al., 1994). However, the ecological validity (i.e., the extent to which a task reflects natural, every-day life conditions) of the tasks mentioned above is limited, because in order to control confounding factors, paradigms become more artificial and may have less predictive validity (Miotto & Morris, 1998; Burgess, Simons, Coates & Channon, 2005; Oosterman, Wijers, & Kessels, 2013; Campbell el al., 2009). To address this problem, some ecological tasks analogous to real-world planning situations have been proposed (Miotto & Morris, 1998; Burgess et al., 2005). Noticeably, Wilson et al. designed the Behavioral Assessment of the Dysexecutive Syndrome battery (Wilson, Alderman, Burgess, Emslie & Evans, 1996) to measure executive functions including a subtest called Zoo Map Task that provides a valid planning ability indicator (Oosterman, Wijers, & Kessels, 2013). Importantly, this subtest provides planning and organizational skills measurement in a more ecological manner. In the present study, in order to evaluate the cognitive planning function, we used an adaptation of Porteus Maze and Zoo Map Task paradigms designed for this study. This behavioral paradigm was composed of a daily life situation divided in four different periods present in cognitive planning: *i)* a planning period, where subjects were asked to plan a paths to visit different locations on a map while monitoring whether the plan being elaborated follows a set of rules; *ii)* a maintenance period, where subjects had to store the planned path in their working memory. Then, *iii)* the execution period, where subjects drew the previously planned route while monitoring and controlling the correct execution. Finally, there was *iv)* a response period, where subjects reported the sequence of animals visited according to their planned path. This paradigm allows measuring different parameters that account for the planning capacity using different stages, including the display of its different components involved (working memory, attentional control, visuospatial analysis, among others) in a manner more analogous to real-life situations, since planning paths on maps is a common daily activity. Furthermore, to control confounding factors, the paradigm considers a control task that has the same structure, the same or similar psychophysical stimuli as the planning task. It demands the implementation of cognitive components that also emerge during cognitive planning (working memory, attentional control, and visuospatial analysis), except the elaboration of a plan per se, since it had a different goal. This allowed adequate isolation of the cognitive planning factor for contrasting the parameters of both behavioral performance and electrophysiological signals.

While the precise brain regions involved during planning are accessible by imaging studies that use fMRI or PET, its fine temporal and neural properties remain elusive. In this study, we address this issue by analyzing neuronal oscillatory activity. We hypothesize that FMθ could be a physiological mechanism of temporal dynamics, reflecting cognitive planning processes (Buzsáki & Draguhn, 2004). Over the past 15 years, there has been an active focus on FMθ activity using scalp EEG assessment, which has been associated closely with several cognitive control functions such as working memory and attentional control. These studies have shown that when subjects engage in processes characterized by goal-directed influence, there is an increase in frontal theta activity (Cavanagh & Frank, 2014; Deiber et al., 2007; Green & McDonald, 2008; Onton, Delorme, & Makeig, 2005; Summerfield & Mangels, 2005; White, Congedo, Ciorciari, & Silberstein, 2012; Raghavachari et al., 2006). Furthermore, FMθ has been posited as a candidate mechanism through which cognitive control might be biophysically performed (Cavanagh & Frank, 2014). However, the dynamic interplay between EEG oscillatory activity and the planning function remains unknown. Under this context, using a novel and experimental ecological paradigm, the present study attempts to answer whether the implementation of cognitive planning induces FMθ activity originating in the PFC, whose sources, via theta activity, are critical for exerting planning.

We hypothesize that the cognitive control implementation during planning is expressed by a significant theta power increase in frontal midline electrodes during the planning period as compared to the control condition, where theta power slightly increases. Additionally, we expect that sources of this theta activity are the PFC regions such as the Anterior Cingulate Cortex (ACC), the mid-Cingulate Cortex (MCC), and the Frontopolar Cortex (FP). The ACC and MCC have shown to be involved in conflict monitoring and attentional control processes, respectively (Orr & Weissman, 2009). Thus, we predict positive correlations between theta activity and behavioral parameters that reflect difficulty in task, i.e., longer latencies of response during the planning period. Finally, we expect that theta activity from FP, which has been shown to participate in generation and monitoring of internally generated stimuli (Christoff & Gabrieli, 2000), correlates with behavioral aspects that reflect better performance in the task such as the percentage of correct responses or more efficient reaction times during the execution of the plan.

2. MATERIALS AND METHODS

2.1. Participants

Data was collected from twenty-seven right-handed healthy adults (13 females) between 19 to 38 years old (mean age = 27.81, standard deviation (SD) = 4.58 years). The sample size was calculated using G*Power 3.1.9.2 software (http://www.gpower.hhu.de/) considering the statistical Wilcoxon signed-rank test, an effect size of 0.7, alpha value of 0.05, and a power of 0.95 (Faul, Erdfelder, Lang & Buchner, 2007). No participant reported neurological or psychiatric disorders according to the MINI-International Neuropsychiatric Interview, Spanish version adapted (Ferrando, Bobes, Gibert, & Soto, 2000). All participants had a normal or corrected-to-normal vision. They were paid CLP$10,000 (approximately USD$15.76 or €13.30) for their participation. The bioethics committee of the Faculty of Medicine of Pontificia Universidad Católica de Chile approved procedures, and all participants signed an informed consent form before the beginning of the study (research project number: 16-251).

2.2. Experimental Design and Procedure

We created a planning task paradigm based on Zoo Map Task (Wilson et al., 1996) and Porteus Maze (Porteus, 1959) programmed in the Presentation Software® by Neurobehavioral Systems (Version 18.0, www.neurobs.com, Neurobehavioral Systems, Inc., Albany, CA) and stimuli were designed using open source SVG tool Inkscape (www.inkscape.org). Using an eye-tracking system (EyeLink 1000 Plus, www.sr-research.com, SR Research, Mississauga, Ontario, CA), we were able to provide participants with real-time on-screen feedback of their eye movements during the task. Simultaneously, we registered the participants brain activity using a scalp EEG system.

The experiment was composed of two conditions: a planning condition and a control condition, each of which included four different periods (see below). These conditions were constructed with a similar structure that allowed control of confounding factors and perceptive components involved in the task and thus, help improve the specific assessment of the processing involved in cognitive planning. Stimuli were projected on an ASUS VG248QE 24" LCD monitor located 82 cm away from the subject.

2.2.1. Planning Condition

The planning condition consisted of 36 trials each with a distinct gray-scale maze that represents a zoo map, preceded by three seconds of a central fixation cross as a baseline. Inside the maze were a gateway and several paths leading to locations of four animals

(**Figure 1A**). Trials were pseudo-randomized. The planning condition was composed of four different periods: planning, maintenance, execution and response (**Figure 2A**).

Planning period: Subjects were instructed to find a path to complete a sequence of visits to all four animals (in any order) according to the following set of rules: (1) Plan the path as fast as possible within a maximum of 10 seconds, (2) Start from the gateway and conclude the path at the fourth animal visited, (3) Do not pass through the same path or corner twice, (4) Do not cross a dead end, (5) Do not cross a path perpendicularly. The planning period was over once the subject pressed a button from a joystick whenever they finished planning or if they exceeded the maximum time. Reaction time (RT) was recorded for further analyses.

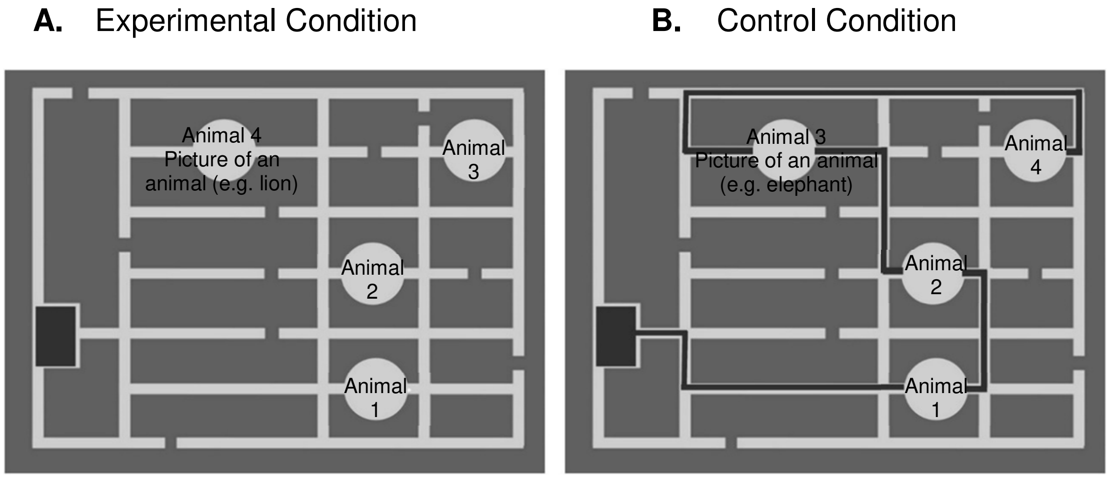


Figure 1. Stimuli of Planning and Control Condition. Illustrative example of the task stimuli is shown. Each stimulus consists of a zoo map with a starting gate, four images of animals located along the maze and different paths that may or may not lead to their locations. During the experimental condition (A) subjects had to plan a path from the gate passing through all animal locations, considering a set of rules. On the other hand, for the control condition (B) a marked line indicating an already existing path was shown (black line*). Here, subjects were instructed to look at this path and figure out whether the rules were followed or not. *The black line presented here is for illustrative purposes. The real marked path was a slightly darker line with low contrast controlled by illuminance (see methods section 2.2.2.) in order to keep the mazes presented in the planning and control conditions as similar as possible. Animals inside of circles were pictures of animals.

Maintenance period: Here, a shifted fixation cross was presented by three seconds. The position of the fixation cross indicated the start position (gate) of the zoo map in order to facilitates the execution of the trace for the next period (see below). During this period, subjects retained in their working memory the plan elaborated in the previous period. Also, this period serves to delimitate the end of the planning period and the beginning of the execution period as an inter-trial interval.

Planning execution period: In this period, the maze was shown again, and subjects were instructed to trace their previous planned path using their gaze through an online eye movement feedback given and registered by the eye-tracker system. Calibrations of the eye-tracker were made at the beginning of the experiment and after every five trials completed. Subjects had a maximum time of 10 seconds to trace the planned path but once they crossed the fourth animal visited, they could finalize by pressing a button. Their RTs were saved for further analysis.

Planning response period: After 10 seconds or upon button press at the end of the execution period, the maze disappeared and only the animals remained on the screen in the same spatial location in which they appeared in previous periods. Additionally, there were four yellow circles at the bottom of the screen. Subjects were asked to insert the animals in each circle following the same order in which they visited them during the execution period. Then, subjects got feedback based on the feasibility of the traced sequence (thumbs-up or thumbs down when the answer was either correct or incorrect, respectively). Paths performed during the execution period were reconstructed offline using the eye-tracker data, then accuracy responses of the traced and planned paths were calculated and used for further analyses (see Supplementary **Figure S1**). Thus, the main goal of the response period was to provide online feedback in order to allow participants monitoring their performance during the task, as well as to keep the motivation to perform the task properly given the rewarding effects of performance feedback (Drueke et al., 2015).

Consequently, the behavioral features used to measure planning performance were the RT during the planning period (the time that subjects needed to figure out how to solve the maze following the rules) and the RT during the execution period (the time that subjects needed to execute the planned trace), and their accuracy, i.e., whether the traced path was feasible or not.

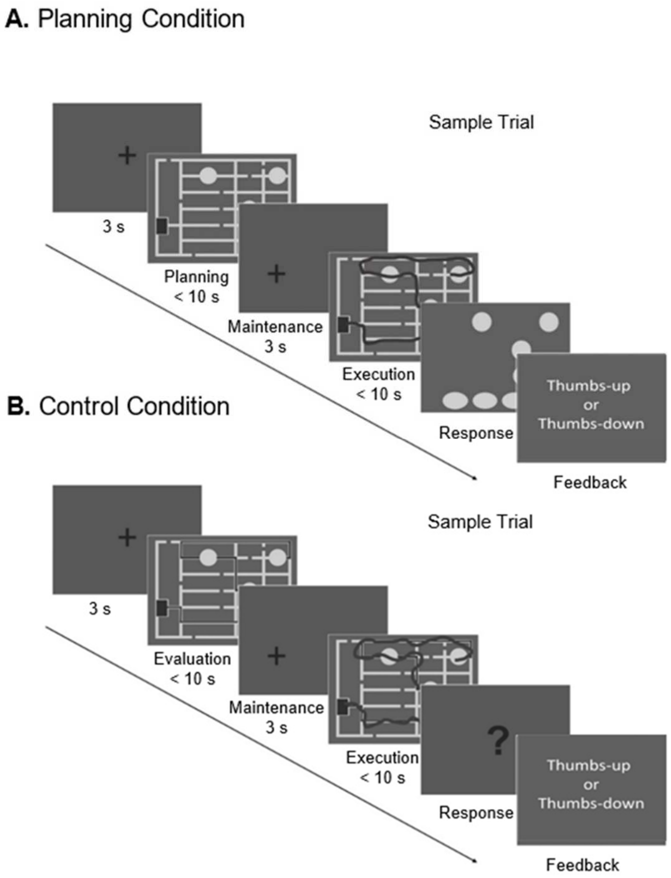


Figure 2. Experimental Design. A) Representative planning condition trial. Planning trial started with a fixation cross presented for 3 seconds. Subjects were then instructed to plan a path visiting all the four animal locations with a maximum time of 10 seconds, following a set of rules (previously explained). Afterward, a shifted fixation cross was shown. Once the maze appeared again, subjects had to execute the trace planned in the previous planning period using their gaze with a visual feedback (given by an eye-tracker system) that delineated their gaze movement in real-time (dark line) with a maximum time of 10 seconds. Then occurred the response period where the subjects had to indicate the sequence made during execution by arranging the animals in the chosen order with a joystick. Based on their response, subjects received feedback (thumbs-up when correct and thumbs-down when incorrect).

B) Representative control condition trial. A fixation cross appeared for 3 seconds. Next, subjects were instructed to look at an existing traced path (dark line) and evaluate whether it followed the rules or not. Next, a shifted fixation cross appeared again after which the maze reappeared. This time subjects had to replicate the already traced route having the same visual feedback as the execution planning period. Next came the response period where they had to answer if the traced sequence followed the previously stated rules or not by pressing a joystick button. Based on their response, subjects received feedback.

2.2.2. Control Condition

Our novel planning task mainly demands the execution of visuospatial planning function, but also requires visuospatial analysis and working memory to some extent (Wilson et al., 1996; Oosterman et al., 2013). In order to control confounding factors, a control task with all the cognitive and perceptual functions needed to solve the planning task was designed, removing the component that elicits the planning function.

The control task had the same structure as the planning task. It consisted of the same 36 distinct mazes. But, each of these presented an already traced path in a slightly darker color with low contrast. This was to keep the psychophysical features of the planning and the control conditions as similar as possible. The illuminance data was measured using a lux-meter positioned in the same chinrest used by the subjects, at the same distance from the screen. No differences in illuminance was found between stimuli of each condition (Planning task stimuli: n = 42, mean = 6.8 lux, SD = 0.14, SEM = 0.02. Control task stimuli: n = 42, mean =6.8, SD = 0.14, SEM = 0.02, unpaired-samples t-test, t (82) = 1.50, p = 0.1397). The traced paths of each maze could either followed the rules or not (**Figure 1B**). Trials were pseudo-randomized. This control task also included four periods: control, maintenance, execution, and response periods (**Figure 2B**).

Control period (guided sequences): Subjects were instructed to look at the mazes which had a traced path from the entrance visiting all four animals. Subjects had to evaluate the traced path and verify whether the sequence followed the rules or not. First, a fixation cross appeared for three seconds. The subject then had 10 seconds to evaluate the traced path. Same as the planning task, subjects could press a joystick button whenever they finished, and the RT was saved for further analyses.

Maintenance: A shifted fixation cross was presented by three seconds. The position of the fixation cross preceded the location of the maze entrance to facilitate the gaze tracing (same as planning condition). In this period, subjects stored in their working memory whether the marked path seen in the previous period followed the rules.

Control execution period: Subjects had 10 seconds to follow the traced path again, overlapping their gaze with the traced path. Once they reached the fourth animal, they could finalize the trial by pressing a button and the RT here was recorded as well.

Control response period: During this period, a question mark appeared, and subjects were asked to answer whether the sequence was correct or not using joystick buttons and the accuracy response was saved. Finally, the feedback was presented, the same as in the experimental condition.

For both the planning and the control condition, subjects were orally instructed by the experimenter using visual aid before starting each condition. Instructions included examples of how to solve the planning and the control condition, respectively. For the control condition, examples of how to evaluate the paths without using any planning strategies (for instance, looking for rule violations of the paths drawn, such as identifying drawings using the same path twice, crossing a dead-end, etc.) were provided. Afterward, a training session of six trials was held for each condition to ensure subjects got familiar with the experiment setup and the goal of each trial condition. Furthermore, after each trial the experimenter asked the participants what strategies they implemented to solve the trial. Then, they received oral feedback about their performance and strategy to make sure that subjects evaluate the paths drawn in the control condition to avoid planning a new path.

2.3. EEG Data Acquisition

Electroencephalography brain activity was recorded using a scalp EEG Biosemi® System (www.biosemi.com) consisting of sixty-four scalp electrodes placed following the 10/20 system, and eight external electrodes. Four external electrodes measured electro-oculography (EOG) activity, two were used for electrocardiogram (EKG), and two for mastoids which were used for referencing later during signal pre-processing. All electrodes were placed according to standard anatomical references (Keil et al., 2014) and referenced to CMS and DRL active electrodes during acquisition. The data was sampled online with a rate of 2048 Hz.

2.4. Data Analyses

2.4.1. Behavioral Data Analysis

Behavioral data were analyzed using custom scripts from MATLAB 8.0 (The MathWorks, Inc., Natick, Massachusetts, United States), SPSS version 22 (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, version 22.0. Armonk, NY: IBM Corp.), and GraphPad Prism version 8 for Windows (GraphPad Software, La Jolla California USA, www.graphpad.com). All behavioral analyses were conducted using the accuracy (percentage rate of incorrect and correct responses) from each condition (the planning and the control condition), and the RT (the average of time spent solving the mazes and evaluating marked paths, and all execution periods) of the first two periods of each condition: the planning period, the planning execution period, the control period, and the control execution period. Additionally, we calculated the RT of each period considering the correct trials only.

Since each condition had two RTs measures and one accuracy outcome, we decided to use an index that can give an integrated measure that accounts for both the RT and the accuracy for each period. This index allowed us to later evaluate the association between electrophysiological signal (theta activity) and behavioral performance properly (see below in 2.4.3. section). Thus, as a new behavioral parameter, we used a performance index that is based on a linear combination of reaction time (RT) and proportion of errors (PE) called the Linear Integrated Speed-Accuracy Score (LISAS) (Vandierendonck, 2018) and is defined as follow:

$$LISAS = RT_j + PE_j \times \frac{S_{RT}}{S_{PE}} \qquad (1)$$

In the above equation, RT_j represented the participants correct RTs (in ms) average of the participants in condition *j*, PE *j* represented the participant's accuracy (in proportion of error) in condition *j*, S_{RT} is the overall correct RTs standard deviation of the participant, and S_{PE} is the overall PE standard deviation of the participant. This equation renders a weighted measure of RT and PE. Thus, an estimate of RT corrected for the number of errors was obtained as a balanced combination of speed and accuracy, which can be interpreted as RT adapted for the percentage of incorrect responses. Hence, LISAS can be considered an integrated index of performance (Vandierendonck, 2018) and it has been proven to be useful when it is known that RT and accuracy might be related or might be the expression of similar or the same cognitive processes (Vandierendonck, 2017, Vandierendonck 2018). To evaluate this, we performed Spearman's rho correlation between RT and accuracy for both the planning and the control conditions (using RT of each period).

To evaluate the internal consistency of the task we computed a Cronbach's Alpha coefficient using RT of each period as input. Additionally, in order to evaluate homoscedasticity, the Levene Test was conducted. D'Agostino & Pearson Omnibus Normality Distribution Test was also conducted in order to choose the proper statistic test in each comparison (parametric or non-parametric). Afterward, depending on the data normality Wilcoxon signed-rank test or matched-paired t-test were performed to compare the difference of the different parameters of behavioral performance between condition periods. These comparisons were conducted to evaluate whether the planning component present in the planning condition was more cognitive demanding than the control condition, and further to find out whether the planning task and the control condition are optimal to evaluate cognitive planning.

Finally, in order to analyze planning with different complexity levels, trials were divided considering the number of valid solutions, being those trials with more than 5 possible solutions considered as ‘easy’ (18 trials) and those with equal or less than 5 possible solutions considered as ‘difficult’ (18 trials). Then, the accuracy and RTs of the planning and the planning execution period were compared between ‘easy’ and ‘difficult’ trials using matched-paired t-test.

2.4.2. Electrophysiological Data Analyses

2.4.2.1. Signal Preprocessing

The EEG data pre-processing pipeline was carried out using EEGLAB toolbox codes (Delorme & Makeig, 2004), EYE_EEG extension (Dimigen, Sommer, Hohlfeld, Jacobs, & Kliegl, 2011), and the ADJUST plugin (Mognon, Jovicich, Bruzzone, & Buiatti, 2011).

Eye movement activity recorded from eye-tracker was synchronized with EEG recordings allowing us to observe the occurrence of fixation, saccades, and blink events, improving the quality of the visual inspection. Co-registration was ensured with shared TTL trigger pulses that were sent from the presentation display computer to the eye-tracker computer during the whole experiment. The sampling rate was downsampled to 1024 Hz and re-referenced to average of electrodes on mastoids. Then, a zero-phase finite impulse response (FIR) filter was used for high-pass filtering, with a high-pass cut-off frequency of 1 Hz and a low-pass cut-off frequency of 40 Hz. The EEG signal was segmented into 36 trials per condition, time-locked to the onset of planning and control periods as epochs of interest. Each trial consisted of 1 s before the start of the maze presentation (as a baseline) and 4 s after the planning or control period, respectively. Subsequently, a second segmentation time-locked to the end of planning and control periods was generated. These epochs consisted of 4 s before the end of planning and control periods, and 1 s of maintenance. These windows length was chosen due to the time to perform each period in the planning and control condition is variable, thus we used the first and the last 4 s of planning and control periods as adequate and sufficient to analyze the oscillatory dynamics without overlapping the first period over the execution period.

Thereafter, Logistic Infomax Independent Components Analysis (ICA) algorithm (Bell & Sejnowski, 1995) was used to identify and remove artefactual components from EEG data. Artefactual components associated with eye movements were rejected based on their covariance with simultaneously recorded eye movement data. This was done using saccade-to-fixation variance ratio criterion between 10 ms pre- and post-saccade (Plöchl, Ossandón, & König, 2012). Additionally, other artefactual components associated to EMG, electrode movement or non-brain-related components were identified by visual inspection. All rejected independent components were also visually validated by inspecting the topographies, spectra, and activations over time.

Finally, noisy channels identified by visual inspection and by automatic channel rejection using kurtosis criterion (5 z-score as threshold) were interpolated using spherical interpolation.

2.4.2.2. Time-Frequency Decomposition

EEG time-frequency analysis was carried out using short-time Fast-Fourier Transform (FFT) for frequencies ranging from 1-40 Hz using a window length of 250 ms and a time step of 5 ms. The time-frequency charts were then z-score normalized to the baseline (-1 to -0.1 s).

Thereupon, electrode Fz was selected for further analyses due to: *i)* The strong increase in theta frequency band seen in frontal midline electrodes (including Fz electrode) shown in topographic maps, and *ii)* the Fz electrode is widely used in frontal midline theta/cognitive control studies (Onton, Delorme & Scott Makeig, 2005; Gartner, Grimm & Bajbouj, 2015; Wang, Viswanathan, Lee & Grafton, 2016). The Pz and Oz electrodes were chosen as controls because they are non-frontal midline electrodes. Afterward, statistical comparisons of time-frequency charts from both conditions, for Fz, Pz, and Oz electrodes, were made through a non-parametric cluster-based permutation test for paired samples, with a p value < .05 at the group-level. The probability of observing a statistically significant effect was calculated using Monte Carlo method with 1000 random draws. The statistic value chosen to perform the permutation test was the maximum statistic value of the cluster (Maris & Oostendveld, 2007).

Theta frequency band (4–8 Hz) from these two different segments was averaged along its whole epoch respectively: 0 to 4 seconds (first four seconds of planning/control) and -4 to 0 seconds (last four seconds of planning/control). Then, averaged theta activity was compared between conditions using a matched-pair t-test or Wilcoxon signed-rank test.

Besides, to analyze the temporal dynamics of theta activity, power in the 4-8 Hz range was averaged across trials by subject. Time profiles of theta band activity for both conditions and the selected electrodes were then compared using Wilcoxon signed-rank test (match-paired, 88 ms steps of non-overlapping windows) and corrected by False Discovery Rate (FDR).

All time-frequency analyses were made using self-written scripts in MATLAB R2014a and R2018b and Statistics Toolbox 8.1 (The Mathworks, Inc., Natick, Masachussets, United States).

2.4.2.3. Source Reconstruction Analyses

Source localization analyses were performed using the open access Brainstorm toolbox (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011), which is documented and freely available for download online under the GNU general public license (http://neuroimage.usc.edu/brainstorm).

Once we observed that there were significant differences in both periods: the first four seconds and the last four seconds between planning and control period, we selected the first four seconds for further analyses. Thus, sources were estimated over the preprocessed EEG signal of the first four seconds of planning (1-40 Hz range, filtered and cleaned) using Standardized Low-Resolution Brain Electromagnetic Tomography (sLORETA) (Pascual-Marqui, 2002). The parameters chosen to perform sLORETA were the minimum-norm imaging method, and the symmetric Boundary Element Method (symmetric BEM) using OpenMEEG toolbox (Gramfort et al., 2010). sLORETA algorithm was conducted on the default anatomical MNI template implemented in Brainstorm ("Colin27") using the default electrode locations for each subject.

We conducted two types of source analysis with different purposes. First, in order to estimate the brain sources of theta activity observed in the scalp electrodes, a bandpass filter between 4-8 Hz was applied over the preprocessed signal. Theta frequency band was selected as a band of interest due to: *i)* There is extensive evidence supporting FMθ as a biophysical mechanism of cognitive control implementation (Cavanagh & Frank, 2014), *ii)* the theta band power increase in midline frontal electrodes observed during visualization of topographic maps, and *iii)* because of the significance difference observed in the planning condition as compared to the control condition in the time-frequency charts and the time profile slices from Fz electrode. Consequently, a z-score normalization was applied using -1000 to -10 ms pre-trial onset as baseline. Then, we averaged the theta activity between 1 and 4 seconds as a time span of interest. The criterion used to select this range of time was based on the theta activity dynamics observed in topographic maps time slices, the time-frequency charts and the time profile slices whose significant increased activity started after 500 ms (see results section). Lastly, averaged space sources were compared between conditions using non-parametric permutation sign test using Monte Carlo Sampling (1000 randomizations) (Tadel et al., 2011).

Second, in order to determine regions of interest (ROIs) associated to planning, cortical areas were labeled according to Destrieux Atlas available in the FreeSurfer Package in Brainstorm toolbox (Destrieux, Fischl, Dale & Halgren, 2010), and ROIs were bilaterally selected based on *i)* significance differences between conditions in permutation tests as well as *ii)* high theta frequency band increase in the planning condition alone, and *iii)* evidence reporting prefrontal cortex regions involved in cognitive control functions (Orr & Weissman, 2009; Christoff & Gabrieli, 2000). These regions included bilateral superior frontal gyri (SF), bilateral transverse frontopolar gyri and sulci (FP), bilateral ACC, and bilateral MCC (Supplementary **Table S1**). Using the previous preprocessed EEG signal (1-40 Hz range, filtered and cleaned) Principal Component Analysis (PCA) was conducted for each ROI's activity and the first mode of the PCA decomposition for each ROI was selected. A spectral estimation using a short-time FFT was performed as indicated in the Time-Frequency Decomposition section and compared between left and right ROI using a non-parametric cluster-based permutation test (Maris & Oostendveld, 2007) following the same procedure and using the same parameters described above at the channel-level. Afterward, each bilateral region presenting no differences between left and right was extracted again as one bilateral time series: SF, ACC, MCC, and then represented in time-frequency charts and compared between conditions. Furthermore, time-frequency charts obtained according to the complexity level of the planning task (easy versus difficult trials) were compared for each ROI. Since the dorsolateral PFC has been described as a crucial region for planning performance and working memory (Nitschke et al., 2017; Barbey, Koenigs & Grafman, 2013), this brain region was also considered for analyses.

To compare the time profile of theta band across conditions, activity from selected ROIs was band-pass filtered between 4-8 Hz and Hilbert Transform was applied to obtain the instantaneous amplitude (Le Van Quyen et al., 2001) using Signal Processing Toolbox from MATLAB software (MathWorks). In order to avoid edge effects created by the band-pass filter, each end of the signal was mirrored using a length of 512 samples before applying the Hilbert Transform. Afterward, the signal was z-scored (using -1000 to -10 ms as baseline) and averaged across trials by subject. Finally, each ROI source activity was compared between conditions using Wilcoxon signed-rank test (matched-pairs, 1 s of non-overlapping windows) and corrected by FDR.

2.4.3. Correlations between Theta Activity and Behavior

In order to test whether there is a relationship between frontal theta activity and planning performance, the eight ROIs source time-series were first z-score normalized by baseline. Then, a window from 1 to 4 seconds after planning/control onset was selected as a period of interest based on relevant theta activity dynamics observed in time-frequency results.

Moreover, based on the extensive evidence of theta activity increase in the ACC and the MCC (Cavanagh & Frank, 2014; Cohen, 2014) canonically associated to slower performance (typically greater RTs) indicating the employment of cognitive control (Gratton et al., 1992; Rabbitt & Rodger, 1977) in a variety of cognitive control functions (Cavanagh et al., 2017; Munneke et al., 2015; van Driel et al., 2015; Frank et al., 2015; van Driel et al., 2017; Cohen, 2016), we chose the bilateral ACC and MCC to evaluate whether their theta activity correlated with slower RT. Additionally, we sought to analyze specific segments of time intervals within the 1 to 4 s window. Thus, we used two additional non-overlapped windows of 1 second each at the second and the third second after the trial onset. We sought to evaluate whether there were specific time intervals with associations with RTs during the planning period. To do this, we selected late time intervals of interest based on the time dynamics of theta activity whose significant increases can be seen between 2-4 s after trial onset.

Subsequently, the source signal was decomposed in the frequency domain (1-40 Hz) using the multitaper method implemented with Chronux toolbox (Bokil et al., 2010) for each period and ROI. Next, the theta frequency band (4-8 Hz) was averaged, and two measures of theta power were calculated: *i)* Δ theta, which was obtained by subtracting the control period theta power ($\boldsymbol{\theta}_{\text{control}}$) from the planning period theta power ($\boldsymbol{\theta}_{\text{planning}}$), and *ii)* the relative increase in theta activity, which is the ratio of the Δ theta (Δ $\boldsymbol{\theta}$) and the control theta activity ($\boldsymbol{\theta}_{\text{control}}$):

$$\Delta\theta = \theta_{planning} - \theta_{control} \qquad (2)$$

$$Relative\ Increase\ in\ Theta = \frac{\Delta\theta}{\theta_{control}} \qquad (3)$$

These two parameters provide information of the theta activity increase in the planning condition with respect to the control condition.

On the other hand, we calculated two behavioral parameters: *iii)* Δ LISAS Planning, which is the subtraction between LISAS Planning and LISAS Control, and *iv)* Δ LISAS Planning Execution, which is the subtraction between the LISAS Planning Execution and LISAS Control Execution:

$$\Delta LISAS_{planning} = LISAS_{planning} - LISAS_{control} \qquad (4)$$

$$\Delta LISAS_{planning\ execution} = LISAS_{planning\ execution} - LISAS_{control\ execution} \qquad (5)$$

These behavioral parameters provide information of the behavioral performance during planning with respect to control condition.

Finally, Spearman's rho correlations were performed using the electrophysiological and behavioral parameters calculated and then corrected by FDR across the total number of tests.

2.4.4. Analysis of Theta Phase Synchrony

To identify theta phase synchrony communication within the PFC brain regions, we first computed individual time-resolved phase-locked activity for each ROI source using the weighted Phase Lag Index (wPLI) (Vinck et al., 2011) as implemented in the Fieldtrip toolbox (Oostenveld et al., 2011). We performed this analysis for frequencies ranging from 1 to 40 Hz using a Hanning multitaper time-frequency transformation and a non-overlapping window length of 100 ms for the epoched trials between -1 to 4 seconds locked to the trial onset of the planning and the control period. Thereupon, the theta band (4-8 Hz) was extracted and the time-resolved wPLI was z-score normalized to the baseline (-1 to -0.1 s). The wPLI was chosen because of its lack of sensitivity to zero phase-lag interactions. Then, we compared time-resolved wPLI values between conditions using Wilcoxon signed-rank test (matched-pairs, 250 ms of non-overlapping windows) and FDR corrected.

2.4.5. Eye Movements analyses

The saccade amplitude and the saccade peak velocity from the whole trial and from 0 to 3.75 seconds of the planning and the control condition were extracted using EYE_EEG toolbox (Dimigen et al., 2011) and then compared using Wilcoxon signed-rank test or matched-paired t-test depending on whether data were normally distributed. The window between 0 to 3.75 seconds was selected to control for potential differences in eye movements that might be present at delays around 3.75 seconds, in which the control condition subjects were close to finishing the trial, and their eye movements were expected to stop. Additionally, the coherence between Fourier EEG power at electrode Fz and saccade rate was evaluated as described in Sato and Yamaguchi (2008). The power-saccade rate coherence values from the first four seconds after trial onset were compared between conditions using Wilcoxon signed-rank test.

3. RESULTS

3.1. Behavioral Results

All behavioral features analyzed showed a normal distribution according to D'Agostino & Pearson Omnibus Normality Test except values of accuracy for the control condition. Supplementary **Table S2** shows a summary of the normality distribution test results.

3.1.1. Reliability

The internal consistency of each task period (the planning, the control, the planning execution, and the control execution period) was excellent according to the categories of reliability proposed by George and Mallery (2003). The Cronbach’s alpha coefficient ranged between .95 and .97 (Supplementary **Table S3**) for RTs as input. These results suggest that each task period has a consistent set of trials indicating high task reliability.

3.1.2. Performance

Table 1 shows a summary of the most relevant descriptive statistics. Variability analysis by the Levene Test showed homogeneity in variance (Supplementary **Table S4**).

Table 1. Behavioral descriptive data for each parameter

Parameters	Descriptive Statistics*			
	Mean	Median	SD	SEM
Planning RT	8846	9145	1150	221.3
Planning Execution RT	6326	6289	1114	214.4
Accuracy Planning	85.70	88.89	7.69	1.48
Control RT	6807	6570	1497	288.1
Control Execution RT	5706	5551	988.9	190.3
Accuracy Control	95.68	97.22	4.77	0.92
LISAS Planning Index	9281	9779	938.2	180.6
LISAS Planning Execution Index	6927	6912	1341	258.2
LISAS Control Index	7117	7023	1466	282.1
LISAS Control Execution Index	5923	5725	1033	198.7
Planning RT 'easy'	8546	8858	1397	268.9
Planning RT 'difficult'	8967	9414	1067	205.3
Planning Execution RT 'easy'	5830	5653	1222	235.2
Planning Execution RT 'difficult'	6547	6680	1076	207.2
Accuracy Planning 'easy'	89.92	94.44	7.55	1.45
Accuracy Planning 'difficult'	81.48	83.33	10.56	2.03

SD = Standard deviation; SEM = Standard error of the mean; RT = Reaction Time; LISAS = Linear Integrated Speed-Accuracy Score. *Values of RT and LISAS are presented in milliseconds. Values of accuracy are the percentage of correct responses.

Furthermore, RTs of different periods were evaluated and compared. The RT of the planning period in comparison to the control period was significantly greater (**Table 1**, Supplementary **Table S5**, **Figure 3A**). The same was observed when the RT of the planning execution period was compared to the execution control period (**Table 1**, Supplementary **Table S5**). This reflected that the planning condition was cognitively more demanding than the control condition. Furthermore, the planning period was also more time consuming than the planning execution period (**Table 1**, Supplementary **Table S5**, **Figure 3B**). Similarly, the RT during the control period was significantly greater than the RT of the execution control period (**Table 1** and Supplementary **Table S5**). In terms of response accuracy, subjects were less accurate during the planning condition as compared to the control condition (**Table 1**, Supplementary **Table S5**, **Figure 3C**) which may also reflect that the planning condition is more complex leading the subjects to perform less accurately.

To analyze whether there is a relationship between RT and response accuracy, we performed Spearman's rho correlation between these behavioral parameters. We found that only the RT of the planning execution period was correlated with the accuracy of the planning condition (Supplementary **Figure S2**, **Table S6**), showing that both may appertain to the same cognitive process.

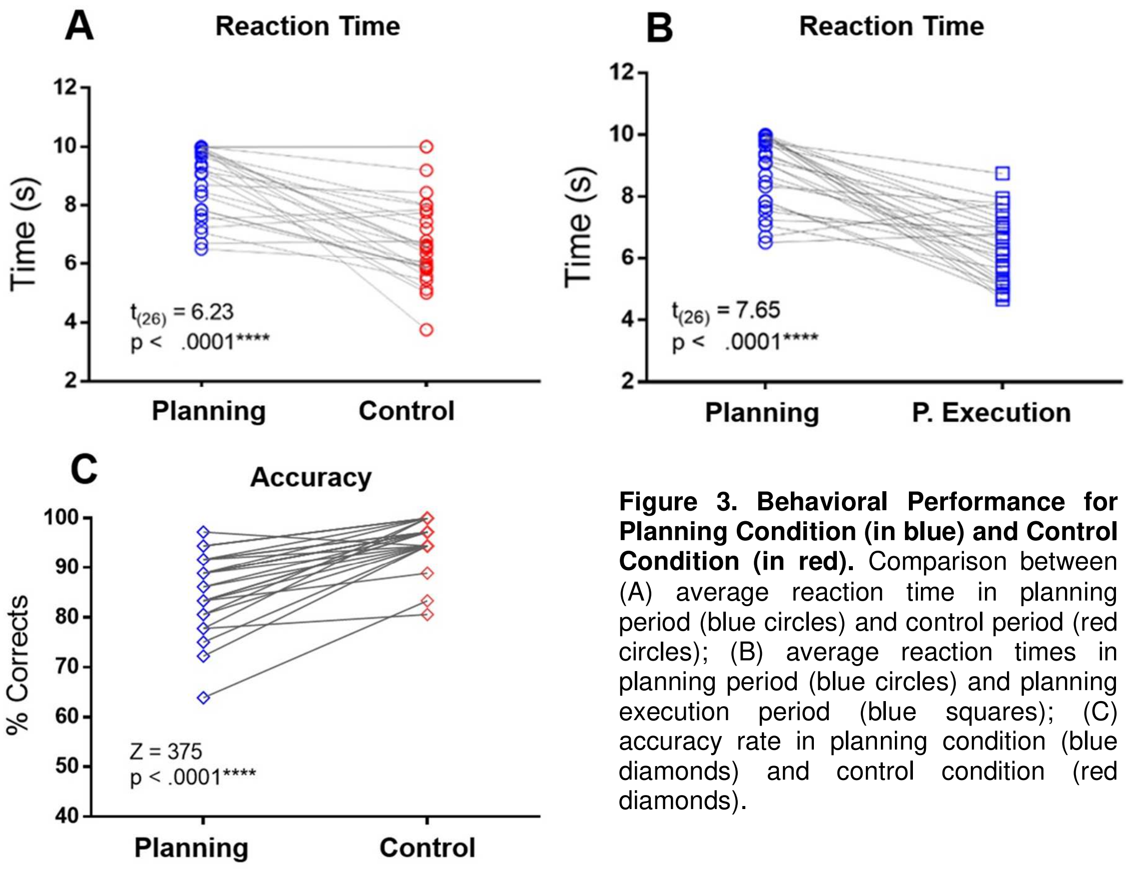


Figure 3. Behavioral Performance for Planning Condition (in blue) and Control Condition (in red). Comparison between (A) average reaction time in planning period (blue circles) and control period (red circles); (B) average reaction times in planning period (blue circles) and planning execution period (blue squares); (C) accuracy rate in planning condition (blue diamonds) and control condition (red diamonds).

Since the RT of the planning execution period and the accuracy of planning are related, we used LISAS to obtain an index that represents the RT corrected for the number of errors (Vandierendonck, 2017; Vandierendonck, 2018). The correlation effect was also present when we used LISAS of the planning execution period (Supplementary **Figure S2, Table S6**), suggesting that LISAS of this period might reflect the association between RT and accuracy as well. Similar effects observed in the behavioral performance comparisons between conditions were obtained when the LISAS performance index was compared to intra and inter-condition (Supplementary **Table S5**).

Additionally, the complexity levels of planning were analyzed. We found there were statistically significant differences between the 'difficult' and the 'easy' level in accuracy and RTs for both the planning and the planning execution period (**Table 1**, Supplementary **Table S5**, **Figure S3).** The 'difficult' level showed greater RTs in the planning and the planning execution condition. Moreover, accuracy for the 'difficult' level was lower than the 'easy' level. These results suggest that separating trials according to the number of valid solutions can discriminate easy trials from the difficult trials.

Collectively, once the planning component was successfully extracted from the control condition, all these behavioral results indicate that the planning condition (both the planning and the planning execution period) is more cognitively demanding. This was expressed by higher RT and lesser accuracy during the planning condition. Therefore, the task conditions, specifically their neural correlates, can also be compared to each other.

3.2. Electrophysiological Results

3.2.1. Frontal Midline Theta Activity

Global theta activity was calculated as follows: Topographic maps from the averaged theta frequency power of the whole epochs (the first and the last four seconds of the planning period and the control period, plus 1 s of their respective maintenance period) across the subjects were visualized. Global theta activity corresponding to the planning period showed a local increase in the frontal midline electrodes (Fpz, AFz, Fz, FCz) in the first 4 seconds, the last four seconds, and the maintenance period, respectively as compared to their control period counterpart where there were not an apparent increase in theta band power. The planning effect was computed as the power subtraction between planning and control periods and showed an increase in theta power that stays consistent in frontal midline electrodes for the planning period (**Figure 4A,** Supplementary **Figure S4**).

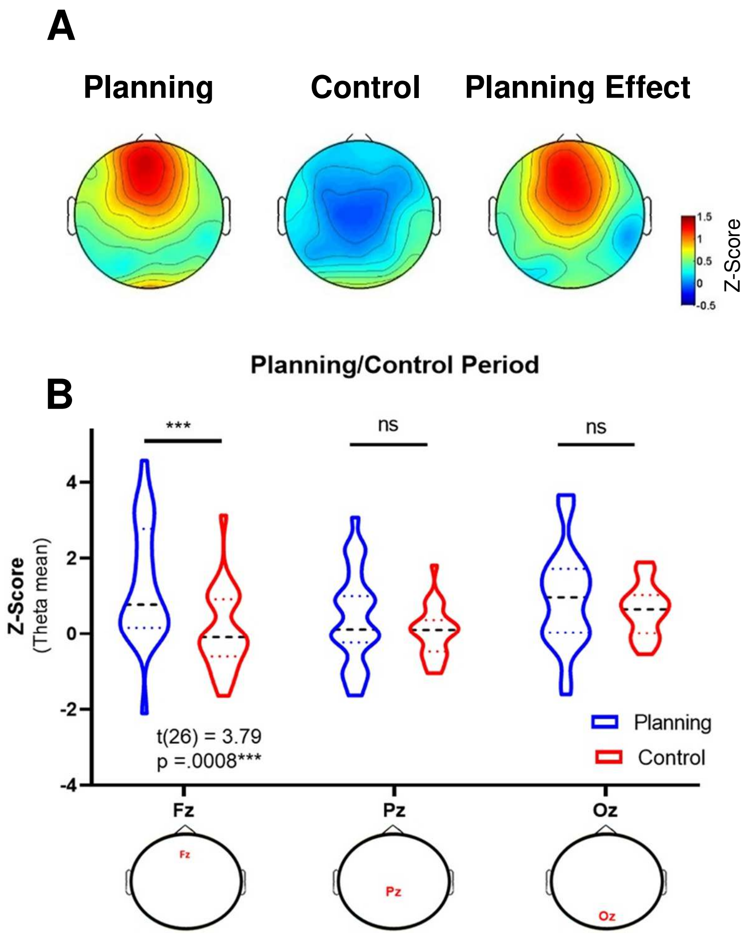
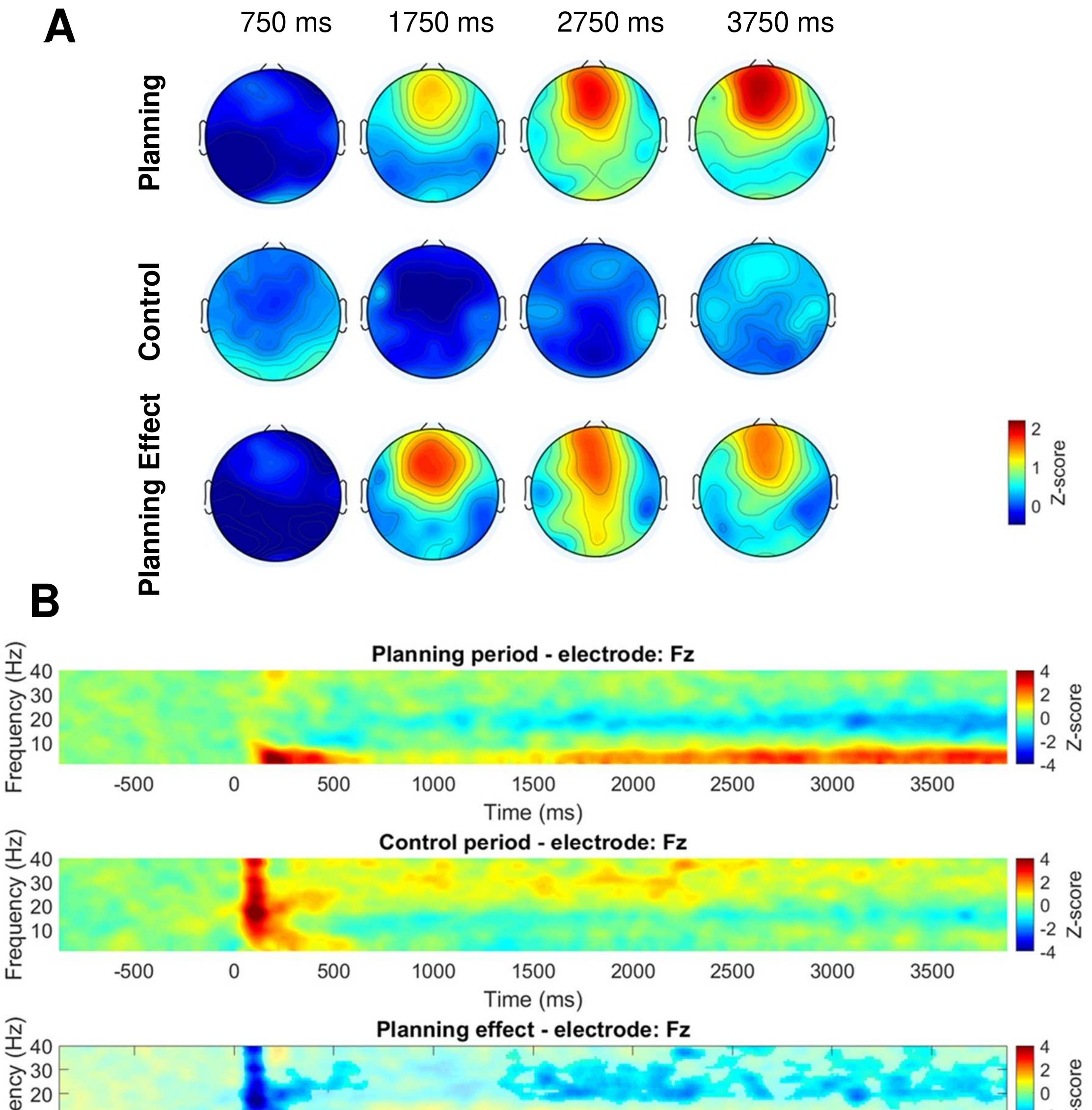


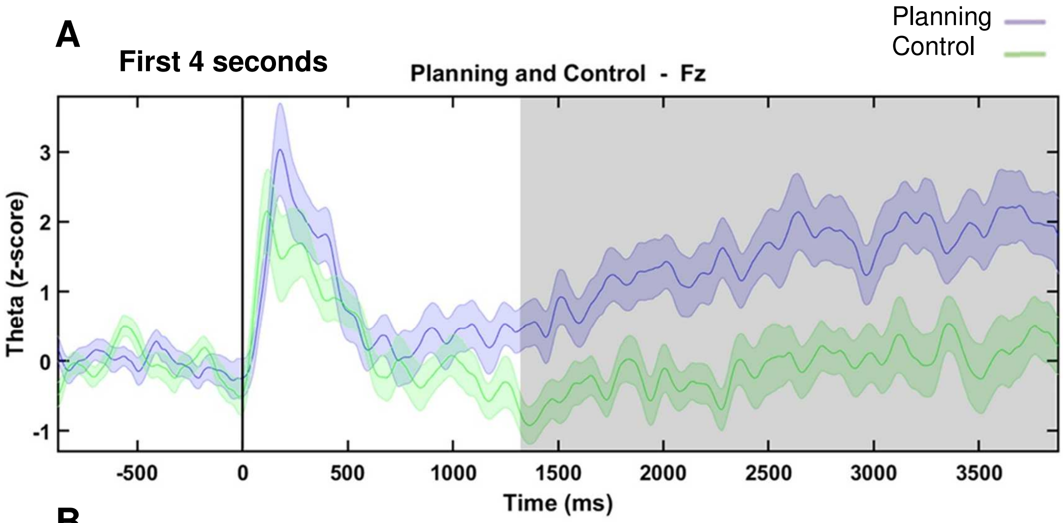
Figure 4. Global FMθ activity during the first 4 seconds of planning. A) Scalp representation of average theta frequency band power across all subjects, normalized to z-score during the planning period (left), the control period (middle) and for the planning effect (right). Left: During the planning period, subjects showed an increase in theta frequency band power located mainly in frontal midline electrodes. Middle: Control period showed no evident increase in the theta frequency band. Right: Planning Effect (power subtraction between periods) illustrates the increase in theta frequency band in frontal midline electrodes. Color bar indicates z values between -0.5 to 1.5. B) Fz average theta band power (left) for all 27 subjects during the first 4 seconds of planning (blue) in comparison to the control period (red) exhibited a significant greater power. In contrast, Pz and Oz did not present significant differences between periods. (see Supplementary **Table S7** and **Table S8**)

To analyze whether this observed increase in global FMθ activity during the whole epochs were significant, the averaged theta frequency band during the first and the last 4 seconds of planning for Fz electrode from the planning period were compared to the control period respectively. Global FMθ activity from Fz electrode during planning showed a significant increase in comparison to global theta activity during the control period in both epochs. However, no significant differences between conditions were found for non-frontal midline electrodes used as controls: Pz and Oz (**Figure 4B**, Supplementary **Table S7-S8**).

Afterward, in order to assess the temporal dynamics of FMθ we observed topographic maps corresponding to specific time points of averaged theta band power (750, 1750, 2750 and 3750 ms). As time progress, a sustained increase in the FMθ activity for the planning period is observed. While theta activity during the control period seems absent (**Figure 5A**). Time-frequency analysis of electrodes Fz, Pz, and Oz for the first and last four seconds of planning revealed increases in low-frequency bands, most importantly a progressive increase in the theta band (4-8 Hz) that starts after 1 second of the planning period onset. This effect was absent in the control period. Time-frequency charts were assessed using a cluster-based permutation test confirming a significant difference between conditions. Clusters suggested differences in the theta band power between periods for Fz, Pz, and Oz electrodes (**Figure 5B**, Supplementary **Figure S4-S8**). Furthermore, negative clusters suggested a power decrease in both alpha and beta ranges during the planning condition when compared to the control condition in Fz electrode (**Figure 5B, Figure S4**), which might be reflecting working memory processes (Lundqvist et al., 2011; Lundqvist et al., 2018) and motor planning preparation as it has been shown in motor control studies (Fairhall, Kirk & Hamm, 2007; Doyle, Yarrow & Brown, 2005). At the beginning of the control period there was a broadband activity specific for this condition. This activity could have been showing evoked activity, an early error detection and/or task-specific evaluation processes which did not affect our analysis and interpretations since the focus of this study and the main comparisons were on late cognitive process (**Figure 5B**). Additionally, the frequency of interest showed a non-significant increase in this early period (0 to 1 second after trial onset) for both conditions as shown later (**Figure 6A**).


A
750 ms
1750 ms
2750 ms
3750 ms
Planning
Control
Planning Effect
2
1
0
Z-score
B
Planning period - electrode: Fz
Frequency (Hz)
40
30
20
10
-500
0
500
1000
1500
2000
2500
3000
3500
Time (ms)
4
2
0
-2
-4
Z-score
Control period - electrode: Fz
Planning effect - electrode: Fz

In order to better characterize the temporal dynamic of the increase in theta frequency band, we then averaged the power between 4-8 Hz for both conditions, obtaining the average band power of theta band over time. We found that the increase in theta activity was significantly greater for the planning period for Fz electrode starting 1 second after the trial onset until subjects stopped planning (**Figure 6**). However, this effect was absent for non-frontal midline electrodes: Pz and Oz electrodes (Supplementary **Figure S9-S10**). This was seen in both time windows: the first four seconds (**Figure 6A**, Supplementary **Figure S9A-S10A**) and the last four seconds of planning and control period (**Figure 6B**, Supplementary **Figure S9B-S10B**). Interestingly, a remarkable increase in theta band was found during the maintenance period of the planning condition, which may reflect storing of the plan in working memory to execute it on the next period (**Figure 6B,** Supplementary **Figure S4**).


A First 4 seconds

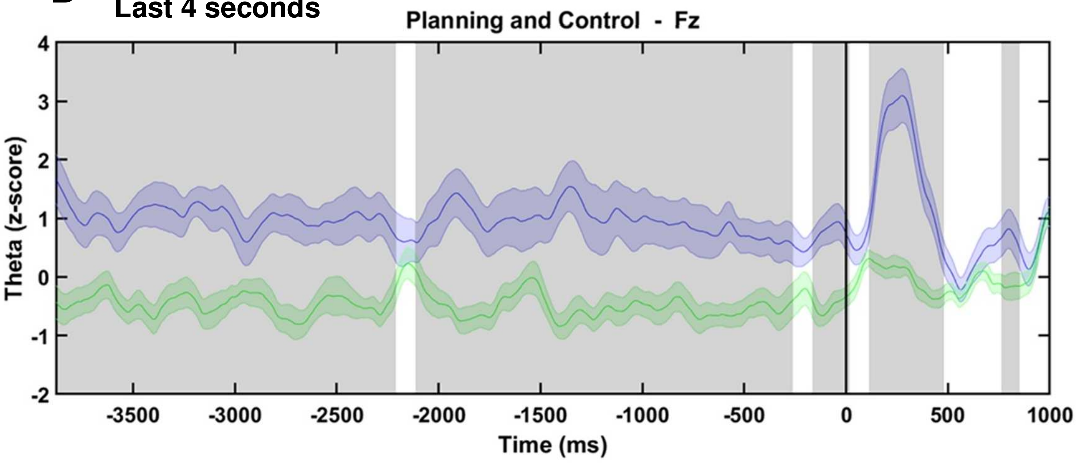
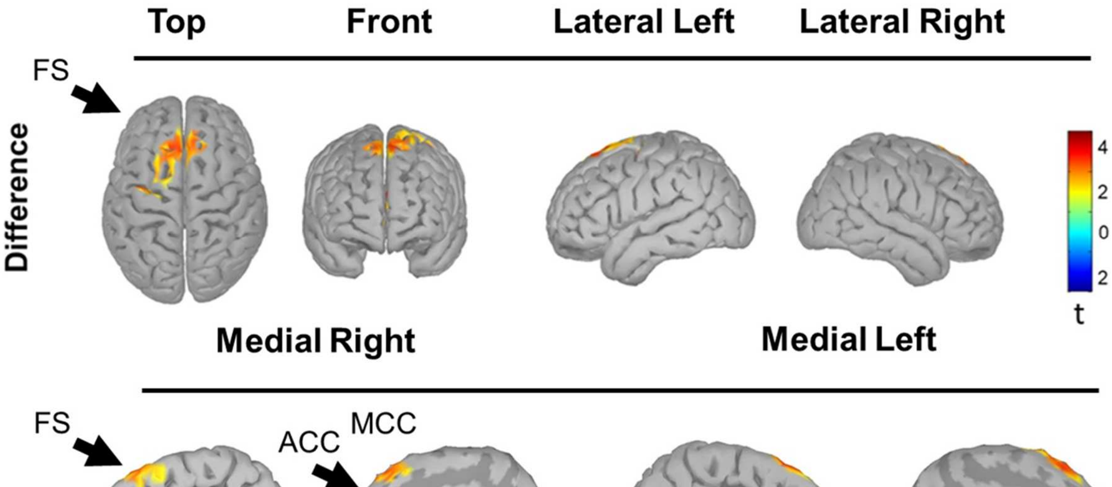

B Last 4 seconds

Figure 6. Time Theta Frequency Slices of Fz. A) Fz first 4 seconds of planning (purple) and control (green) period showing a significant and progressive increase of theta activity

3.2.2. Source Reconstruction Results

In order to localize the sources, we visualized the whole brain model template and cortical activations for both conditions. We found a specific activation in prefrontal areas for planning (bilateral left FP, bilateral ACC, and bilateral MCC), and right-occipital and right-temporal activations for the control period (Supplementary **Figure S11**). However, significant differences between conditions were found in the PFC (the bilateral SF, the bilateral ACC, and the bilateral MCC) (**Figure 7**) being higher for the planning period. Furthermore, to analyze the time frequency domain we performed spectral estimation of ROI time series. ROI time series were calculated using the first mode of the PCA decomposition of all the signals from a ROI. Time-frequency charts were then obtained by using a short-time window FFT. Subsequently, time-frequency charts were compared between bilateral ROIs and periods using non-parametric cluster-based permutation tests (**Figure 8**, Supplementary **Figures S12-S15**).



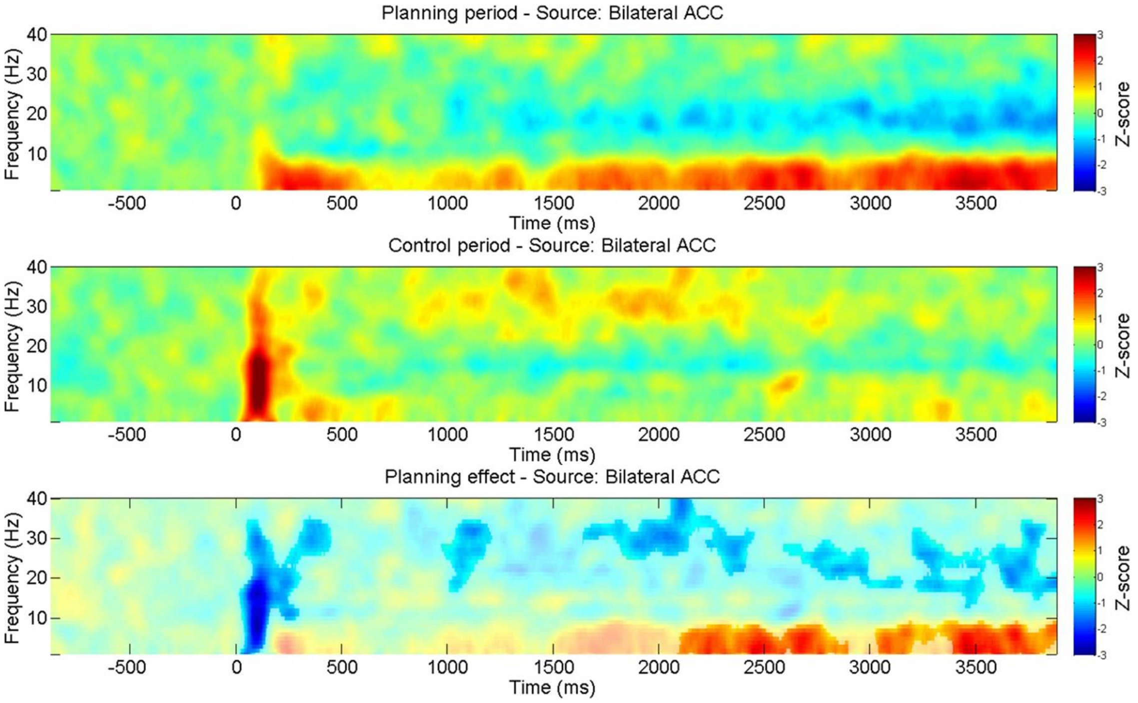
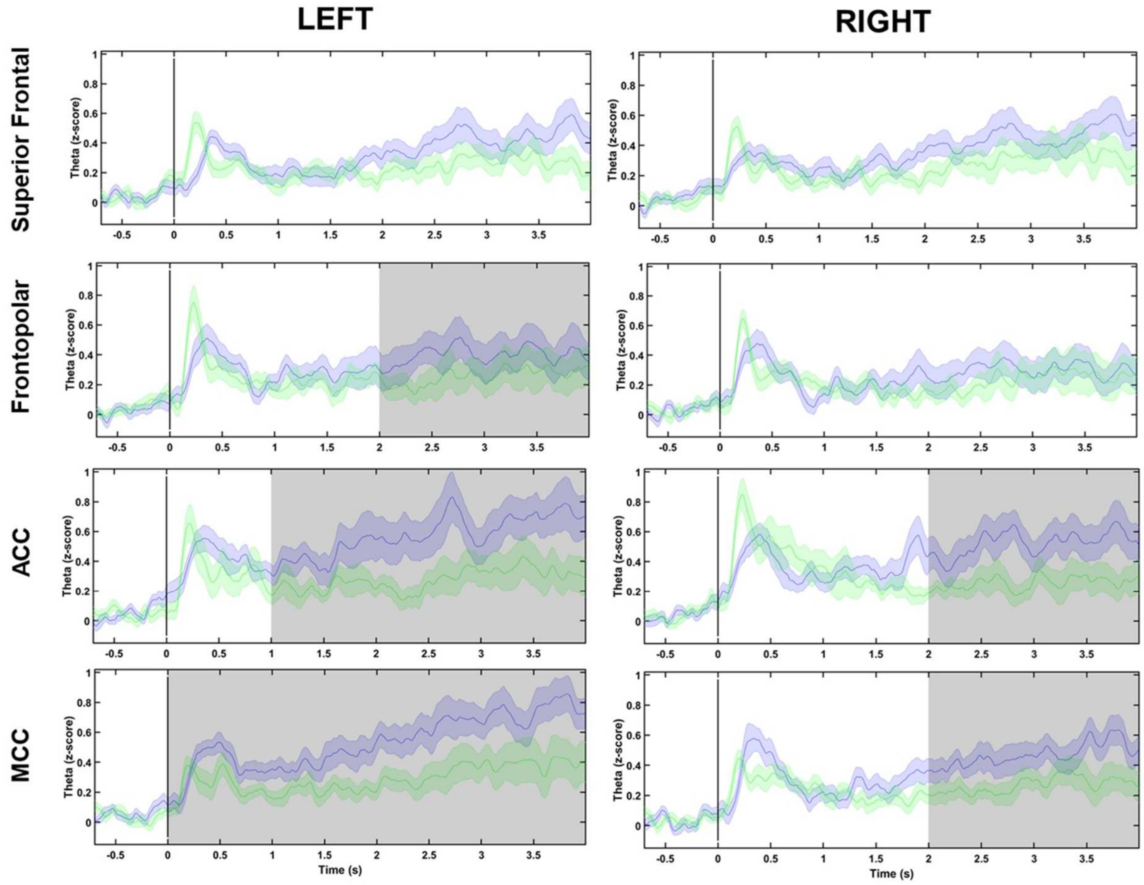


Figure 8. Time-Frequency charts for bilateral ACC Source. Top: Time-frequency plot for the planning period showing a marked increase in theta band power over time. Middle: Time-frequency plot for the control period. Bottom: Planning effect computed as the subtraction between planning and control period showing significant differences in theta activity after 2 seconds. Also, an early decrease in broadband frequencies is observed. Non-significant pixels are shown lighter in the plot. Color bar indicates units of z-score values between -3 to 3. ACC: Anterior Cingulate

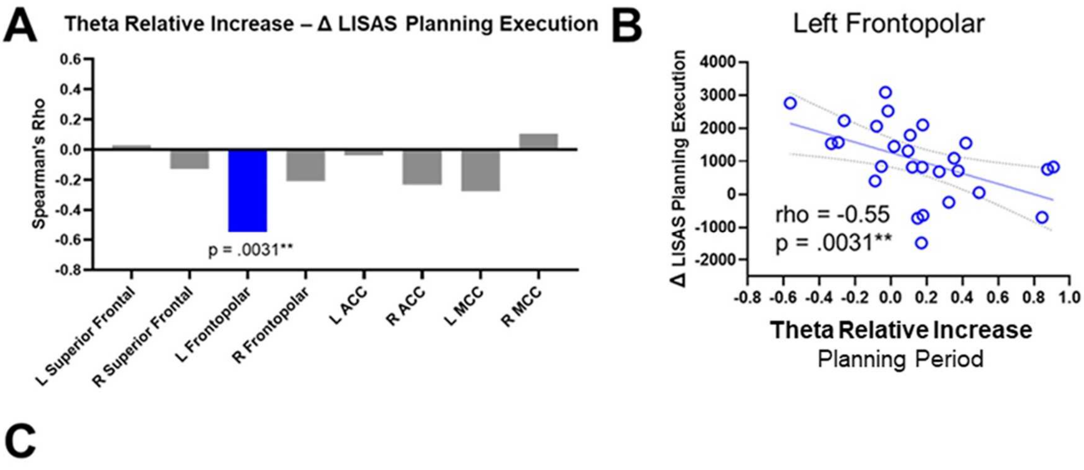
The left FP source (**Figure S14**) and the bilateral ACC (**Figure 8**) presented significant differences between planning and control period. The positive clusters suggested theta power increase during planning. Additional analysis on the bilateral dorsolateral PFC source was done and there were significant differences on the beta band which may reflect working memory engaging during planning (Lundqvist et al., 2011; Lundqvist et al., 2018) (Supplementary **Figure S16-S17**). Afterward, to confirm these results and evaluate theta changes over time, we performed a Hilbert Transform for each ROI time series separately (left and right) after which we compared the amplitude of theta frequency between conditions. We found that the left FP source presented significantly higher theta frequency band power between 2-4 seconds after the planning period onset. This was also exhibited by the bilateral ACC and the bilateral MCC in different time points of the planning period. The left ACC showed increase in theta amplitude since 1 second after the planning period onset. Similarly, the right ACC and the right MCC exhibited increase in theta amplitude after 2 seconds after the planning period onset. The left MCC presented a significant increase in theta power for the whole epoch (**Figure 9**). Together, these results suggested that during cognitive planning the aforementioned PFC regions engaged in theta band.



Finally, we sought to evaluate whether the spectral features during planning can be different according to the level of complexity as shown in the behavioral results. Interestingly, we found that there was a significant difference in the left ACC in the alpha band. Hence, this contributed to the idea that the planning task assesses more intrinsic aspects of planning reflected in theta oscillation changes than other general cognitive demands typically present in cognitive control tasks (Supplementary **Figure S3**).

3.3. Correlations between Theta Activity and Planning Performance

To evaluate the relationship between the theta activity of cognitive planning and the planning performance, we performed Spearman's rho correlations using the theta relative increase from ROIs source and the Δ LISAS Planning or Δ Planning Execution as described in methods section. We found a negative correlation: higher the left FP Theta relative increase (its Δ theta activity as well) during the planning period, lesser the Δ LISAS Planning Execution (**Figure 10A-B**). There were no correlations between the dorsolateral PFC source and planning performance (Supplementary **Table S9-S10**). We found results in the same line using the RTs of correct responses of the planning execution period (Supplementary **Table S11**).



Since, on the one hand different time points exhibited significant increases in theta activity in time-frequency charts and time profile slices of theta activity in late periods during planning. On the other hand, midfrontal theta increases have been related to slowing in RT, we evaluated the Δ theta time dynamics correlations with the Δ LISAS Planning in two time-windows for the bilateral ACC and the bilateral MCC. We found the right MCC and the left ACC exhibited positive correlations: higher their Δ theta activity power, greater the Δ LISAS Planning during the planning period in the 2-3 s specific time interval (**Figure 10C**). Thus, the right MCC and the left ACC may play a pertinent role when the mental elaboration of a plan is being developed, while the left FP may become more involved to execute a plan successfully, which may suggest a differentiated role for theta activity and determined brain regions while cognitive planning processes are exerted compared to when the plan is executed.

3.4. Theta Phase Synchrony

To assess theta activity synchronization within PFC brain regions we analyzed time-resolved theta phase connectivity using the wPLI for each period and each pairwise ROI interactions. Results showed a significant theta phase synchrony increase between the right MCC and the right ACC in late segments after trial onset during planning. Furthermore, brief segments during the control period also exhibited theta phase synchrony increases but in earlier segments after trial onset for the left FP and the right FP cortex interactions. These results suggest that theta dynamics at the level of phase synchrony were present differentially between conditions in terms of PFC brain regions communication involved and their temporal computation for planning processes (Supplementary **Figure S18**).

3.5. Eye movements and Theta Activity.

The different goal and cognitive demands of each condition might prompt different types of eye movements in the planning versus the control condition which in turn could induce different patterns of oscillatory activity (Staudigl et al., 2017; Thaler et al., 2013). In order to address this issue, we first inspected the data at the level of single-subject and single-trial at different levels. Importantly, Fz row time series and the theta activity time dynamics seemed not related to the saccade rate over time (**Figure 11A**).

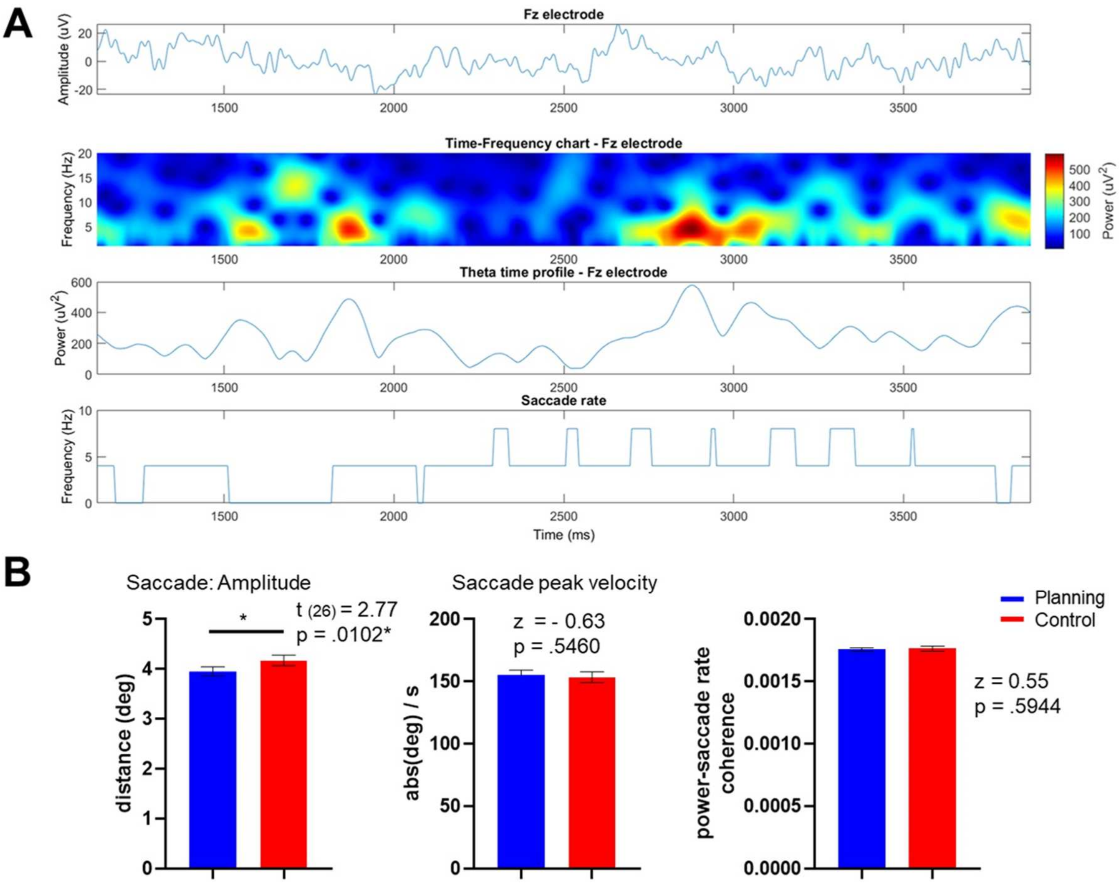


Figure 11. Results of EEG signals and eye movement recordings. A) Row EEG, time-

Second, we extracted the saccade amplitude and the saccade peak velocity from the whole trial (Supplementary **Figure S19**) and from 0 to 3.75 s being then compared (**Figure 11B**). For both periods we found that saccade amplitude was greater during the control condition. On the other hand, the coherence between Fourier theta power at electrode Fz and saccade rate was compared and there were no statistically significant differences between conditions (**Figure 11B**, Supplementary **Figure S19**) reflecting that any possible relation between saccades and theta activity is not different between conditions.

4. DISCUSSION

In this study, EEG activity was recorded during a novel and ecological planning task to evaluate whether cognitive planning implementation, as a higher-order cognitive control function, induces FMθ activity originating in PFC regions, and whether these sources are related to different aspects of planning performance. To address these questions, we designed a novel planning task with adequate psychometric properties in terms of reliability and variability.

There are studies that have assessed the reliability of planning tasks (Wilson et al., 1996; Porteus, 1959), however, there have not been any reports on psychometric properties needed for the adaptation of planning tasks for neuroimaging assessment (Kirsch et al., 2006; Tremblay et al.,1994) at least within the scope of our literature review. In this study, excellent reliability was found for the behavioral task outcomes in the two conditions: planning and control (Supplementary **Table S3**). Additionally, the task's behavioral parameters showed a normal distribution (Supplementary **Table S2**) and variance homogeneity (Supplementary **Table S4**).

Typically, behavioral paradigms used in cognitive neuroscience research are presented in lab-based sensory deprived settings using oversimplified stimuli, in order to avoid confounding factors that might interfere in the understanding of cognitive phenomena as much as possible (Miotto & Morris, 1998; Zaki & Ochsner, 2009; Shamay-Tsoory & Mendelsohn, 2019). For this reason, the brain mechanisms of several cognitive functions, including high-order cognitive functions such as planning, are lacking. There are two main limitations in studies using such tasks, *i)* the person-dependent factor, which establishes that artificial tasks may limit the active role of the participants in paradigms affecting their sense of agency and embodiment; *ii)* the situation-dependent factor, which states that the artificial context where participants perform on tasks might engage different mechanisms than what a real-life context would demand (Shamay-Tsoory & Mendelsohn, 2019). As a result, current trends in cognitive neuroscience encourage and promote experimental designs with greater ecological validity, since this might bring more extrapolatable findings to understand the brain mechanisms underlying human cognition (Caine, 2002; Kingstone, Smilek, Ristic, Friesen, & Eastwood, 2002; Zaki & Ochsner, 2009). Taking these factors into account, in this study we have designed a behavioral paradigm based on the Zoo Map and Porteus Maze Tasks that allowed the measurement of the planning function in a controlled setting. There are several trade-offs in our design. While our novel planning task sticks to a deprived lab-based setting, the task is enriched with meaningful stimuli and goals. The behavioral paradigm was composed of a planning task that demanded the behavioral performance of a task analogous to a daily life situation, and which was divided into different periods that are present during cognitive planning. In our study, the bulk of the analyses were focused on the planning phase and the execution phase because they compound the main phases of planning function: In the first period, subjects have to plan a path while monitoring whether it follows a given set of rules, and then a second period where they store it in working memory. Subsequently, there is a third period in which subjects must carry out their former plan while monitoring the path's behavioral execution, making sure the path follows these rules. While planning and executing the plan, subjects must have enough cognitive flexibility to correct the trajectory adequately if planned or traced incorrectly. Thus, the task demands implementing cognitive control functions in a concerted manner as it may occur in real-life situations, where planning paths on maps are part of everyday life. For this reason, we decided to evaluate the planning function using this paradigm over other traditional and well-established planning tasks (such as the Tower of London or Tower of Hanoi-based tasks). Additionally, an ecological task design requires the paradigm to demand subjects to exert cognitive planning that an actual daily life situation would demand (Miotto & Morris, 1998; Burgess, Simons, Coates & Channon, 2005; Morris & Ward, 2005). However, the ecological validity of a task can range from artificial set-ups to real life situations, as shown in Shamay-Tsoory & Mendelsohn (2019). Accordingly, we argue that our task is a more ecologically valid task than the traditional neuropsychological tasks used to assess planning, where subjects meet an abstract and fictitious setting. Despite the fact that our task might not reflect a real-life scenario completely, we believe that planning trajectories is certainly more meaningful and similar to what people do in their daily routines.

Moreover, designing an ecological-behavioral task not only has to be analogous to a real life situation but also requires predictive validity, i.e., that the task must be able to identify impaired planning function in patients with psychiatric or cognitive disorders who exhibit impaired planning performance in their daily life (Oosterman, Wijers, & Kessels, 2013). This was another reason of why our novel paradigm was based on the Zoo Map Task, which has been shown to have optimal predictive validity in previous studies (Oosterman, Wijers, & Kessels, 2013). Therefore, designing an adequate control task that effectively isolates the planning component was essential, and this is reflected in the results obtained in both behavioral and electrophysiological measures. Because the control condition required subjects to achieve a goal in a task that included the same stimuli but did not require planning, the planning component was successfully removed. Due to this removal, we observed FMθ activity induced by cognitive planning during the planning period, which was not observed in the control period.

The behavioral results for the planning condition were in line with our predictions. Since the planning task implies a high cognitive function (Lezak, 1995; Zwosta, Ruge & Wolfensteller, 2015), we predicted higher RTs and less accurate performances during the planning condition (complex task: plan a path in a complex map) than during the control condition (simple task: they only have to follow a marked path and decide whether it followed the rules). Moreover, in both periods of the planning condition (the planning period and the planning execution period) RTs were always higher than the control condition (the control period and the execution control period) reflecting how difficult and cognitively demanding the planning condition is (Owen, Doyon, Petrides & Evans, 1996; Voytek et al., 2015; Ossandón et al., 2012). Interestingly, the execution of the planned path (during the planning execution period) involved a considerably more cognitive effort during the planning task, as suggested by higher RTs during the planning execution period compared with the control condition periods (the control period and the control execution period, Supplementary **Table S5**). This can be explained by the requirement of high cognitive functions such as working memory and attentional control to perform the execution of the plan. All these observations are in line with the theoretical assumption of cognitive planning (Hayes-Roth & Hayes-Roth, 1979; Wilensky, 1983; Grafman & Hendler, 1991; Zwosta, Ruge & Wolfensteller, 2015).

Although the control condition was designed to measure less complex cognition as evidenced by better performances and faster processing times, and then to compare it against the planning condition, it was favorable to use planning tasks with different complexity levels and analyze planning function according to this. It was possible to identify behavioral differences between the ‘easy’ condition and the ‘difficult’ condition with any differences at the level of electrophysiological measures, suggesting that results account for intrinsic aspects of the planning function more than general features of cognitive control such as attention, cognitive effort, or high cognitive demand. However, this is unusual and further studies controlling different levels of complexity might be helpful to clarify this point.

Previous studies have reported that PFC has a critical role during cognitive planning (Kirsch et al., 2006; Newman, Carpenter, Varma, & Just, 2003; Owen, Doyon, Petrides & Evans, 1996; Nitschke et al., 2017) and the present results show that cognitive planning induces a FMθ activity (**Figures 4-6,** Supplementary **Figure S4**) originating in the PFC, specifically the ACC, the MCC, and the SF (**Figure 7**). These results are in line with previous studies on higher-order cognitive functions (Cavanagh & Frank, 2014; Hanslmayr et al., 2008; Cavanagh, Frank, Klein & Allen, 2010; Cohen & Cavanagh, 2011). Extensive evidence supports the role of FMθ activity as a common top-down mechanism for realizing the need for cognitive control (Cavanagh & Frank, 2014; Cavanagh, Zambrano-Vazquez & Alen, 2012; Cooper et al., 2019). FMθ activity, as a marker of cognitive control, is thought to be exerted by recruiting and aiding communication between brain regions during tasks that require active cognitive engagement (Cavanagh, Cohen & Alen, 2009; Cavanagh & Frank, 2014; Sauseng, Tschentscher, & Biel, 2019).

Although few studies have attempted to deepen the understanding of the temporal dynamics of FMθ activity, most of them agree that its time profile could reflect different mechanisms of cognitive control and the different PFC areas involved for it (Cooper et al., 2019; Sauseng, Tschentscher, & Biel, 2019; Bartoli et al., 2018; van Driel, Swart, Egner, Ridderinkhof, & Cohen, 2015). Here, we characterized the FMθ activity time profile for the planning condition as more demanding and therefore requiring a higher extent of cognitive control. The control condition was characterized as demanding cognitive control to some extent but less than the planning condition. The FMθ temporal dynamic activity during the planning condition was characterized as an increase between the 4-8 Hz band that progressively grows over the first four seconds and then was kept increased over the last four seconds. On the other hand, the control condition showed just a transient stimulus-locked broadband increase showing no theta band increase over time (**Figures 4-6,** Supplementary **Figure S4**).

Here, we have shown that, for the first time, as other executive functions, FMθ also emerges during cognitive planning, and its temporal dynamics may be a marker of cognitive control. Additionally, source analysis confirmed that the primary sources of this FMθ activity are: SF, FP, ACC, and MCC (**Figures 7-9**, Supplementary **Figures S11-S15**).

The SF region is located in the superior part of the PFC and it has been described to be involved in a variety of functions associated to cognitive control functions, i.e., working memory (Boisgueheneuc et al., 2006, Owen, 2000; Owen et al., 1998, Petrides, 2000), attention (Corbetta, Patel & Shulman et al., 2008, Fox et al., 2006) and sensorimotor control-related tasks (Chouinard & Paus, 2010, Martino et al., 2011, Nachev, Kennard & Husain, 2008). Since planning requires working memory and attention, the FMθ activity observed in this region may reveal the participation of these higher-order cognitive functions to support the process of planning. Furthermore, the SF region is anatomically and functionally connected to the dorsolateral PFC and the cingulate cortex through the cingulum (Beckmann et al., 2009).

In the case of the FP region, it has been associated to higher cognitive functions, for instance, it becomes active during working memory, self-generated stimuli, planning, problem-solving and reasoning tasks (Braver & Bongiolatti, 2002; Baker et al., 1996; Christoff & Gabrieli, 2000). In this study, we observed discernable associations between these brain regions and different parameters of planning performance, for e.g., a higher theta relative increase from the left FP for elaborating a plan (the planning period), and a reduced Δ RT (corrected by incorrect responses) for executing a plan previously planned (the planning execution period) were correlated. Consistently, these results were replicated when RTs of the correct responses during the planning execution period were replicated. This particular result is relevant, since most evidence in cognitive control study have shown that frontal theta predicts reaction time slowing in cognitive tasks (Cooper et al., 2019). In this case, theta activity from the left FP might be related to efficiency and accuracy, because quicker execution of plans was associated with accuracy (Supplementary **Figure S2**), this result is in line with studies that showed frontal theta predicts specific cognitive control-induced behavioural changes beyond general reaction time slowing (Cooper et al., 2019). There is extensive evidence showing that the FP cortex participates in monitoring and manipulating information internally generated such as in planning task, inductive reasoning, tasks that require a plan generation or monitoring of self-generated stimuli (Berman et al., 1995; Baker et al., 1996; Osherson et al., 1998; Goel et al, 1998; Christoff & Gabrieli, 2000), Additionally, it has been shown that the FP is involved in monitoring the relevance of alternative goals to replace the current one (Mansouri et al., 2017). Thus, we interpreted that during cognitive planning the left FP is recruited to elaborate a plan and to monitor different alternative paths while keeping the goal in working memory to successfully execute the plan which might be expressed in better reaction times. The ACC and the MCC have been associated with cognitive control (Cavanagh & Frank, 2014), i.e., conflict monitoring (Botvinick, Cohen, & Carter, 2004; Kerns et al., 2004; Sohn et al., 2007, Ursu et al., 2009), error detection (Carter et al., 1998; Gehring & Fencsik, 2001, Pourtois et al., 2010), response selection (Turken & Swick, 1999; Awh & Gehring, 1999; Paus, 2001), and attentional control (Aarts & Roelofs, 2011; Orr & Weissman, 2009; Crottaz-Herbette & Menon, 2006; Luo et al., 2007). Additionally, the MCC plays a role in regulating the autonomic nervous system, nocifensive and rewarded behaviors, multisensory orientation of the head and body in space (Amiez & Procyk, 2019; Vogt, 2016). Evidence have shown a differentiated role for the ACC and the MCC for minimizing distraction (Orr & Weissman, 2009). The MCC is involved in attentional control and the ACC in conflict detection. Consequently, in the context of cognitive planning, while the ACC might be recruited for conflict monitoring like verifying selected paths to be used, the MCC could be contributing to exert attentional control which in turn ended up in RTs increases as seen in this study. Overall, the right MCC and the left ACC may play a pertinent role when the mental elaboration of a plan is being developed, while the left FP may become more involved to execute a plan successfully, and theta activity could be the biophysical mechanism to exert these cognitive control functions.

Interestingly, differences in other frequency bands such as alpha and beta were also observed at channel and source-level. We believe that these variations might express the enriched spectral nature of the brain functions in terms of coordination and communication within and between regions (Canolty & Knight, 2010; Fell & Axmacher, 2011). For instance, Sadaghiani and Kleinschmidt suggested three brain networks involved in cognitive control that modulate alpha oscillations influencing local signal processing, disparate information exchange, and behavior (2016). Specifically, the alpha activity from the ACC and the MCC might reflect the cingulo-opercular network engagement proposedly provide an updating mechanism for incoming signals supporting and maintaining tonic alertness or vigilance through cortical alpha oscillations to exert attentional control (Sadaghiani et al., 2010; Sadaghiani et al., 2015). On the other hand, decreased prefrontal beta oscillations were observed in time-frequency charts during planning. Recent studies have suggested that beta oscillations have a role in executive functions such as working memory (Lundqvist et al., 2011; Lundqvist et al., 2018). Specifically, it has been shown that beta drops during encoding and before response, when the stored information is needed (Lundqvist et al., 2018). We interpreted that during planning, beta suppression might be acting as an inhibitory filter, controlling working memory components and expressing similarities with motor preparation beta (Schmidt et al., 2019; Fairhall, Kirk & Hamm, 2007; Doyle, Yarrow & Brown, 2005) to execute the plan in the next period. Further analyses need to be done to clarify the role of these oscillations during cognitive planning and the possible interaction between theta and alpha/beta oscillations at the level of cross-frequency synchrony phase-amplitude coupling.

One major limitation of the present study is the differences in saccade amplitude during the planning period compared to the control period (**Figure 11B**, Supplementary **Figure S17**), which could lead to introducing artifacts in the EEG signal (Thaler et al., 2013). However, several studies proposed a direct relationship between different eye-movements parameters and specific cognitive phenomena. For instances, Bodala et al. (2016) showed that, along with a decrease in frontal midline theta, saccade amplitude and velocity also decrease with decrease in sustained attention and, Velasques et al. (2013) found that the saccade amplitude produces oscillatory changes in the frontal gamma band in a prosaccadic attention task. It has also been shown that the amplitude of occipital alpha band activity predicts the impact of eye-movements (blinks and saccades) in a perceptual task (Nakatani et al., 2013). Thus, saccade amplitude (along with other eye-movement parameters) might reflect different cognitive mechanisms instead of solely adding confounding noise to the EEG signal. In the present study, we improved the detection of eye-movement related artifacts by ICA method using the saccade-to-fixation variance ratio criterion between 10 ms pre- and post-saccade (Plöchl, Ossandón, & König, 2012). This criterion optimizes the artifact removal process for free viewing tasks (see Dimigen, 2020). Additionally, there were no differences in saccade peak velocity and no differences in theta power-saccade rate coherence between conditions. However, further studies to address these questions are strongly recommended.

Altogether, we postulate that the FMθ activity from the PFC, and the implementation of working memory, attention, and monitoring function, might be aiding cognitive planning by contributing to the dynamic internal elaboration of a plan and its motor execution. These results are in agreement with the consensus of the existence of cognitive control core functions (Lehto, Juujärvi, Kooistra & Pulkkinen, 2003; Miyake et al., 2000) like working memory, inhibitory control, attention, upon which higher-order cognitive control functions such as reasoning, problem-solving and cognitive planning are built (Collins & Koechlin, 2012; Lunt et al., 2012).

5. CONCLUSIONS

The present study evaluated a novel cognitive planning task with behavioral and electrophysiological measurements. Results suggest that the proposed planning task is optimal to evaluate planning, and that it induced FMθ activity originating in the PFC. We characterized for the first time both the spatial and temporal dynamics of this activity during planning. A specific association between theta activity from the left FP and planning performance was found, which may reflect the participation of this brain region in a successfully self-generated plan. Furthermore, the associations between theta activity from the right MCC and the left ACC with reaction times of the planning period may reflect high cognitive demand of the task, engaging in attentional control and conflict monitoring implementation. The findings in this work are in accordance with the broad body of evidence supporting the role of local FMθ activity in cognitive control.

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